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Wild bee diversity in two sites of tropical dry forest in central Mexico

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Abstract

Bee communities are strongly dependent on the floral resources provided by vegetation; hence, factors that affect floral availability also affect bee communities. In this study, we compare bee diversity and seasonality between two localities in the Tropical Dry Forest (TDF) of central Mexico. We quantified the vegetation cover at each locality using satellite imagery and compared it between localities using linear models. At each locality, we sampled wild bees over one year, covering two rainy seasons and one dry season. Bees were sampled using entomological nets, focusing on understory vegetation. Association of bee abundance with each season and locality was tested using a chi-squared test. Diversity was estimated using Hill numbers, and species composition was analyzed using non-metric multidimensional scaling. Diversity and composition were compared across localities and seasons. We collected 1,076 bees of 148 species, 55 genera, and five families. The most abundant families were Apidae and Megachilidae. There were no significant differences between sites in the diversity of any of the orders. The diversity of the three orders was significantly higher at both localities during the 2015 rainy season. Our results indicate that Mexican TDF is rich in bee species. However, the differences in community composition between localities and the current deforestation rate of these habitats imposes challenges to effectively preserve bees in the tropical dry forest.

Keywords

Apoidea, Hills numbers, seasonality

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Introduction

Within the framework of global biodiversity loss, the decline of insect pollinators is especially concerning (Potts et al. 2016; Estrategia Nacional para la Conservación y Uso Sustentable de Polinizadores en México [ENCUSP] 2021). Bees are one of the most important insect groups in the world in terms of both frequency and performance in pollinating crops and natural vegetation (Michener 2007). Bee decline has been widely documented for managed species (e.g., *Apis mellifera*) (Smith et al. 2014) and is related to threats including habitat loss, pesticide use, diseases and parasites, and climate change (Vanbergen and The Insect Pollinators Initiativeet 2013). Long term studies have indicated that wild bee communities in temperate zones are also decreasing (Senapathi et al. 2015). Although long-term monitoring of bee communities is still sparse in tropical regions in comparison with temperate ones (Vanbergen and The Insect Pollinators Initiativeet 2013), it is likely that wild bees are also declining in the tropics due to similar pressures (Freitas et al. 2009). Given the global insect pollinator decline and the gap in the knowledge of bee diversity in the tropics, there is an urgent need to document basic information on tropical bee communities.

Bee communities rely on vegetation for essential floral resources, making them sensitive to changes in floral availability. Consequently, any factors that impact the availability of these resources are expected to influence bee communities. In tropical dry forests, bee abundance has been shown to correlate with precipitation regimes, which consist of strongly contrasting rainy and dry seasons (Poveda-Coronel et al. 2018; Flórez-Gómez et al. 2020). Interestingly, there have been contrasting findings in this regard: some studies have found that bee abundance and diversity rise during the rainy season and decrease during the dry season (Poveda-Coronel et al. 2018), whereas other studies report the opposite pattern (Flórez-Gómez et al. 2020). These contrasting findings may be the result of differences in the flowering phenologies of specific plants in each of the communities studied (Flórez-Gómez et al. 2020). Hence, seasonal variation in bee abundance cannot be easily generalized across all tropical dry forest habitats, and documenting seasonal fluctuations in bee abundance is basic to understand the structure of the bee community in a specific tropical dry forest habitat.

Second, habitat disturbance, resulting in a decrease in vegetation cover, has also been implicated in modifying bee communities. However, bee diversity and bee abundance have been found to respond differently depending on the type and level of disturbance (Winfree 2010). In a study in tropical lowland forests, it was found that the most disturbed habitats, due to modifications to primary vegetation, tended to have greater bee diversity at the lower canopy and shrub level than undisturbed habitats, but undisturbed habitats had higher total bee abundance (Liow et al. 2001). However, in another study, bee diversity increased in conserved tropical dry forest in comparison with croplands and urbanized areas (Razo-León et al. 2018). Understanding how communities of wild bees respond to specific types of disturbances is crucial, as such disturbances can directly affect their habitat, foraging resources, and nesting sites. Different disturbance factors, such as habitat fragmentation, agricultural practices, or urbanization, may lead to varied outcomes (Winfree et al. 2010) in the bee community

and species composition. Recognizing different patterns in bee communities is a first step for implementing effective bee conservation strategies.

This study was carried out in tropical dry forest; this ecosystem is widely distributed and is highly heterogeneous in both topography and plant community composition (Trejo 2005). Tropical dry forests are highly endangered around the world, and in Mexico, only 29% of original tropical dry forests remained as primary forest in 2004 (reviewed in Portillo-Quintero and Sanchez-Azofeifa 2010). In the state of Morelos, the annual rate of loss is 1.3% (from 1973 to 1989) (Trejo and Dirzo 2000). The main activities that threaten dry forests in Mexico are agriculture, extensive cattle ranching, timber extraction, and deforestation for human settlements (Trejo and Dirzo 2000; reviewed in Portillo-Quintero y Sánchez-Azofeifa 2010).

Studies of the Mexican melittofauna have been conducted in some sites (Vergara and Ayala 2002), but there is a large gap in basic knowledge of the bee communities of tropical dry forest in Morelos. Our objective was to assess bee diversity and seasonality by sampling over the course of one year the bees associated with understory vegetation at two localities of the tropical dry forest in central Mexico. One of these localities has been impacted by transformation of the primary tropical dry forest to croplands and induced pasture used for livestock grazing, while the other locality is part of the natural protected area Reserva de la Biosfera Sierra de Huautla (REBIOSH) and has a lower incidence of agriculture and livestock. We compared bee communities between the localities and seasons and explained our results in light of the herbaceous vegetation cover at each location, estimated by means of a vegetation index (MSAVI).

Materials and methods

Study localities

This study was conducted in two localities in the southern part of Morelos State within the Balsas River Basin in central Mexico (Fig. 1A, B). The climate is warm subhumid (Awo" (w) (i) g), the driest of the subhumid climates found in Mexico (García 2004). Precipitation is approximately 900 mm annually and occurs from May through October (see the climograph from Valencia-Esquivel et al. 2022), with peak rainfall in July and September, frequently with a dry period in August (CONANP 2005). The dry season occurs from November to April. Most of the conserved tropical dry forest of Morelos is protected within the natural protected area Sierra de Huautla Biosphere Reserve (REBIOSH) (CONABIO and UAEM 2006).

Primary vegetation in both localities is tropical dry forest (Fig. 1C). The tropical dry forest in Mexico has seasonal phenological patterns driven by precipitation and drought. This pattern influences water and light availability, and leaf loss among trees (Lopezaraiza-Mikel et al. 2014). Although plant seasonal patterns are marked, they can be highly heterogeneous among sites, since they are directly dependent upon microenvironmental conditions (Kornás 1977). In addition, floristic composition and the plant physiognomy are highly variable across sites (Dorado et al. 2005). Despite this floristic variability, there

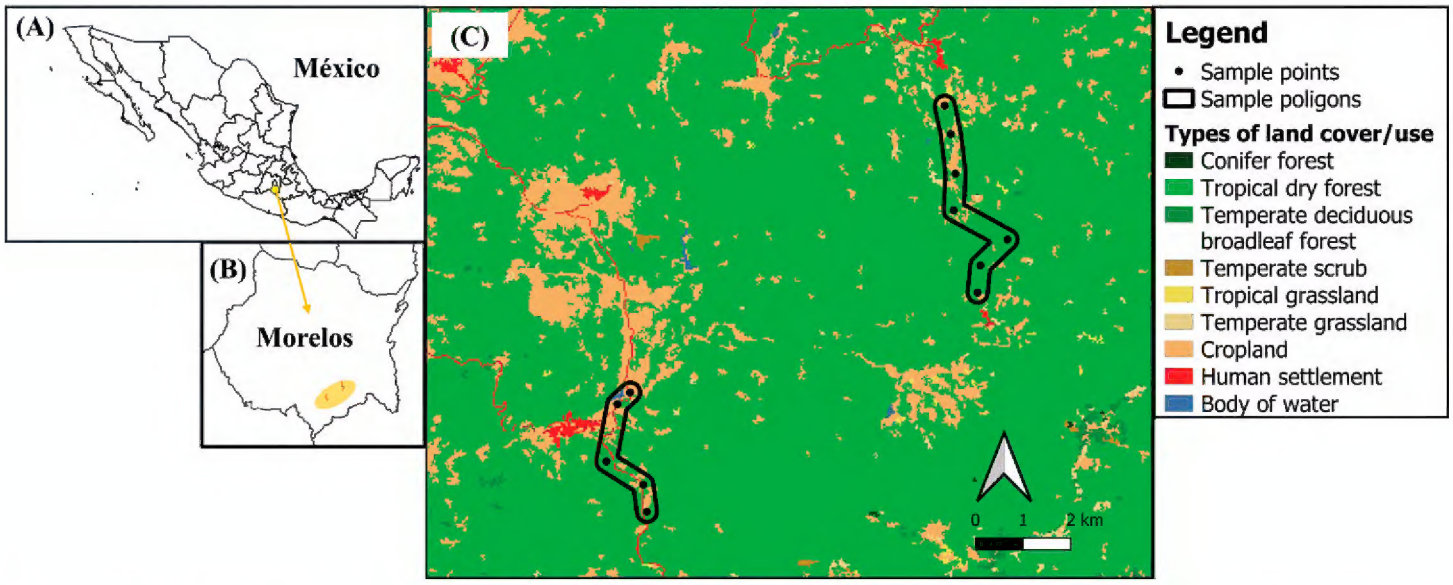

Figure 1. Map of working sites. Map of Mexico (**A**) showing the state of Morelos (**B**) in yellow. The yellow oval shows the approximate location of the two study sites in southern Morelos State (**B**). Land use and vegetation map (CONABIO 2020) showing the Quilamula study site on the left and El Limón on the right (**C**). The legend indicates the meaning of each color, as well as the meaning of the points and polygons.

are several plant species that are consistently dominant in primary dry forest, including *Conzattia multiflora*, *Lysiloma divaricatum* (Fabaceae) (López-Reyes 2019), and several *Bursera* (Burseraceae) and *Ceiba* (Bombacaceae) species (Arias et al. 2002).

The locality of El Limón corresponds to the surroundings of the Biological Station "El Limón" within the REBIOSH (18°32'32"N, 98°56'09"W). Although this locality is within the Reserve and is characterized by continuous vegetation cover, it has some disturbance due to grazing, small-scale agriculture and activities related to the conservation of the white-tailed deer (Velarde-Ebergenyi and Cruz-León 2015). However, these activities are highly regulated by legislation, hence the forest is relatively well conserved. In contrast, the locality of Quilamula (18°29'39.68"N, 99°0'18.02"W), part of the Tlaquiltenango municipality, has only 31% of its surface within the REBIOSH; our study sites were not part of the reserve. Quilamula has a greater proportion of transformed tropical dry forest due to grazing, agriculture, and human settlements than El Limón (Fig. 1). The study sites of Quilamula were located at the edges of a village, within an area with intermingled pasturelands for grazing, secondary vegetation (represented by *Acacia* sp. and *Prosopis* sp.), and conserved, primary dry forest. At both localities, grazing and agriculture convert primary dry forest into secondary vegetation, mainly characterized by sparse understory vegetation.

Vegetation cover

At each locality, we selected sites for bee sampling with understory vegetation that were accessible (7 sites at El Limón, and 5 sites at Quilamula). These were relatively close to each other, so that collectors could visit all sites in one day at each locality. To characterize the vegetation cover of each locality, we used the Modified Soil Adjusted Vegetation Index (MSAVI). The MSAVI is preferred over other indices for character-

izing the sparse vegetation of the tropical dry forest because it relates to the leaf area index in the tropical dry forest (Kalacska et al. 2005) and is more accurate for differentiating the understory vegetation from bare soil in semi-arid ecosystems than other vegetation indices (Purevdorj et al. 1998; Xue and Su 2017). For example, MSAVI is used in agriculture to remotely assess initial crop growth (Voitik et al. 2023). Given that bee sampling was conducted around each of these sites, a polygon 450m wide was drawn around each locality's sampling sites in the program QGIS (Fig 1C). Within each polygon, 98 points separated from each other by ≥ 150 m were placed to serve as sample units (Fig. 1C). For each polygon, the rasters of the average MSAVI at a resolution of 30m were obtained from Climate Engine (Huntington et al. 2017).

Given the biological differences of the tropical dry forest between seasons, we calculated the average MSAVI for three periods that comprised the duration of the study: rainy season (July–October 2015), dry season (November 2015 – April 2016), and rainy season (May–July 2016). To compare the MSAVI between localities, we performed a linear mixed model (LMM), where the response variable was the MSAVI of the 98 random points, the fixed effects were the localities and seasons, and the random effect was the identity of the sample point. By visualizing the residuals, we determined that the LMM met the statistical assumptions of normality, homoscedasticity, and independence. We used R (R Core Team 2022) to perform the analyses, the packages lme4 (Bates et al. 2015) to perform the LMM, and car (Fox and Weisberg 2019) to assess the statistical assumptions of the LMM.

Bee sampling protocol

Bee sampling was conducted monthly at both localities from July 2015 to July 2016. Due to logistical constraints, we did not sample in December 2015. Each month, sampling was conducted during one day from 9:00 to 16:00 by two collectors who traversed all of the sampling sites at each locality; sampling days were sunny and without rain. The entomological nets used were constructed with a light mesh fabric (McCravy 2018), with a diameter of 30 cm and 1 m handle. The two collectors wandered across vegetation that had flowers and was accessible; thus, we conducted haphazard sampling that was focused on the understory vegetation, mainly shrubs and herbaceous plants. Trees were also sampled when flowering branches were accessible. As our study was focused on wild bees, individuals of *Apis mellifera* were not collected. Captured bees were killed with ethyl acetate. One specimen per species was deposited in the Entomological Collection of the Center of Zoological Studies of the University of Guadalajara (JAL. INV. 109.0401). Bee identification was conducted by HEF-L.

Bee community analyses

Abundance of wild bees was obtained by family and compiled per month and season. In order to relate bee seasonality with environmental data, we compared bee abundance with monthly precipitation of each locality. Precipitation data were obtained

from the nearest weather stations to the study localities (Valle de Vázquez – number 17065 for Quilamula, and El Limón – number 17057). These data are available from the National Meteorological Service (2021). To determine if there was a relationship among bee abundance, locality and season, we constructed a 6×4 contingency table (three seasons per each of the two localities, and four bee families; Colletidae was not included due to the low counts obtained). Standardized residuals were calculated to determine whether bee abundance per family differed than that expected by chance across localities and seasons (Agresti 2007). According to Agresti (2007), those standardized residuals > |3| indicate that values in the corresponding cell if the contingency table are greater (positive values) or lower (negative values) than expected by chance.

Sample coverage (i.e., the probability that a newly collected individual belongs to a species that has already been recorded; Chao and Jost 2012) was estimated for each locality and season. Diversity was quantified using Hill numbers (Jost 2006) for each locality and season, as well as for each of the six bee communities – one for each season (2015 rainy season, dry season, and 2016 rainy season) in each locality. Hill numbers are the diversity components (qD) of orders 0D (species richness, which is insensitive to species abundance and assigns high weight to rare species), 1D (exponential of Shannon entropy, which considers the relative abundance of species), and 2D (inverse of Simpson diversity, which assigns a higher weight to abundant species than 0D and 1D) (Hill 1973; Jost 2006). To evaluate differences among localities, seasons, and the six bee communities, rarefaction curves of each diversity order were constructed with 95% confidence intervals (R Core Team 2017). Sample coverage, Hill numbers and rarefaction curves were obtained using the iNEXT package for R (Chao et al. 2014; Hsieh et al. 2016). Finally, to compare species composition across localities and seasons, we used multivariate analyses. The six bee communities were ordered by non-metric multidimensional scaling (NMDS) using an abundance similarity matrix and the Bray-Curtis index as a distance metric. Then, a non-parametric permutation procedure (ANOSIM) was used to determine whether bee composition differed across bee communities. The ANOSIM was based on a matrix of bee abundance by species in each community, using the Bray-Curtis index as a distance metric and 9999 permutations (Hammer et al. 2001). Pairwise ANOSIMs were performed between all pairs of communities as a post-hoc test. These multivariate analyses were conducted in Past (4.03).

Results

The MSAVI was higher in El Limón than in Quilamula pooling across seasons (P = 0.0003). Croplands in Quilamula occupied a more extensive area in the obtained polygon and at the landscape scale. Meanwhile, in El Limón the tropical dry forest was more continuous at both scales (Fig. 1C).

A total of 1,076 bees from 148 species and 55 genera were collected (Table 1). These belonged to five families (Andrenidae, Apidae, Colletidae, Halictidae and Megachilidae). El Limón had higher total abundance (622 bees from 107 species and 50 genera) than Quilamula (454 bees from 99 species and 42 genera; Table 2).

Table 1. Bee species collected in two localities of the tropical dry forest of Morelos, Mexico.

Species	El Limón		Quilamula	
	Female	Male	Female	Male
Andrenidae				
Andrena (*Callandrena*) sp. 1	1	0	1	0
Andrena (*Callandrena*) sp. 2	1	0	0	0
Andrena (*Callandrena*) *manifesta* Fox, 1984	0	0	1	0
Andrena (*Callandrena*) *micheneriana* LaBerge, 1978	7	0	0	0
Andrena (*Callandrena*) *solivaga* LaBerge, 1967	0	0	7	0
Calliopsis (*Calliopsis*) sp. 1	0	1	2	1
Mesoxaea tachytiformis (Cameron, 1901)	0	0	9	0
Protandrena (*Heterosarus*) sp. 1	0	1	0	2
Protandrena (*Heterosarus*) sp. 2	0	0	0	2
Protandrena (*Protandrena*) *eclepta* Timberlake, 1976	3	0	2	0
Protandrena (*Protandrena*) *punctulata* Timberlake, 1976	0	1	0	0
Protandrena (*Protandrena*) *tessellata* Timberlake, 1976	0	0	2	0
Protandrena (*Pterosarus*) *illustris* (Timberlake, 1967)	4	0	0	0
Protandrena (*Pterosarus*) sp. 1	3	1	1	0
Protandrena (*Pterosarus*) sp. 2	0	1	28	3
Protandrena (*Pterosarus*) sp. 3	0	0	0	1
Protandrena (*Pterosarus*) sp. 4	1	0	0	0
Protandrena (*Pseudopanurgus*) *crenulata* (Cockerell, 1905)	1	0	0	0
Apidae				
Anthophora (*Mystacanthophora*) *capistrata* Cresson, 1878	1	1	0	0
Anthophora (*Micranthophora*) *squammulosa* Dours, 1869	0	0	1	1
Anthophorula (*Anthophorsica*) aff. *morgani* Cockerell, 1914	0	0	0	3
Anthophorula (*Anthophorula*) *interrupta* (Timberlake, 1980)	0	0	1	0
Bombus (*Thoracobombus*) *steindachneri* Handlirsch, 1888	33	0	3	0
Centris (*Paracentris*) *agameta* Snelling, 1974	1	5	0	0
Centris (*Centris*) *eisenii* Fox, 1899	0	4	1	0
Centris (*Paracentris*) *griseola* Snelling, 1984	0	0	0	1
Centris (*Heterocentris*) *nitida* Smith, 1874	5	1	2	0
Centris (*Heterocentris*) *transversa* Pérez, 1905	10	0	0	0
Centris (*Heterocentris*) *trigonoides* Lepeletier, 1841	0	0	7	0
Centris (*Centris*) *varia* (Erichson, 1848)	5	1	1	0
Ceratina (*Calloceratina*) *belizensis* Baker, 1907	0	0	3	0
Ceratina (*Calloceratina*) sp. 1	6	0	8	0
Ceratina (*Ceratinula*) aff. *zeteki* Cockerell, 1934	4	1	0	0
Ceratina (*Ceratinula*) *arizonensis* Cockerell, 1898	1	0	0	0
Ceratina (*Zadontomerus*) aff. *strenua* Smith, 1879	22	0	0	0
Ceratina (*Zadontomerus*) sp. 1	6	0	1	0
Ceratina (*Zadontomerus*) sp. 2	5	0	4	0
Ceratina (*Zadontomerus*) sp. 3	1	2	0	0
Ceratina (*Zadontomerus*) sp. 4	14	1	5	0
Diadasia sp. 1 (aff. *D. knabiana*)	0	2	10	1
Diadasia sp. 2 (*D. australis complex*)	11	2	0	1
Epeolus obscuripes Cockerell, 1917	0	1	0	1
Epeolus sp. 1	0	1	0	0
Epicharis (*Epicharana*) *elegans* Smith, 1861	1	0	1	0

Species	El Limón		Quilamula	
	Female	Male	Female	Male
Epimelissodes (*Epimelissodes*) *aegis* (LaBerge, 1956)	0	0	0	2
Epimelissodes (*Epimelissodes*) *albocollaris* (Cockerell, 1918)	0	0	0	1
Epimelissodes (*Anthedonia*) *comptus* (Cresson, 1878)	1	0	1	0
Euglossa (*Euglossa*) *viridissima* Friese, 1899	1	2	0	0
Eulaema (*Apeulaema*) *polychroma* (Mocsáry, 1899)	1	0	0	0
Exomalopsis (*Stilbomalopsis*) *birkmanni* Cockerell, 1922	9	0	2	0
Exomalopsis (*Stilbomalopsis*) *solani* Cockerell, 1896	0	3	0	0
Exomalopsis (*Exomalopsis*) sp. 1	0	0	2	0
Exomalopsis (*Stilbomalopsis*) sp. 2	0	0	2	1
Exomalopsis (*Exomalopsis*) sp. 3	0	0	2	0
Exomalopsis (*Phanomalopsis*) sp. 4	1	0	0	0
Frieseomelitta nigra (Cresson, 1873)	1	0	36	0
Habropoda sp. 1	1	0	0	0
Melissodes (*Eumelissodes*) *druriellus* (Kirby, 1802)	2	0	4	0
Melissodes sp. 1	0	0	0	2
Melissodes (*Melissodes*) *tepaneca* Cresson, 1878	5	3	11	5
Melissoptila otomita (Cresson, 1879)	0	0	1	0
Melitoma marginella (Cresson, 1872)	1	1	0	3
Mesocheira bicolor (Fabricius, 1804)	1	0	0	0
Nomada sp. 1	0	1	0	0
Paratetrapedia (*Paratetrapedia*) *flavescens* Aguiar & Melo, 2011	1	1	0	0
Paratetrapedia (*Paratetrapedia*) *mexicana* Aguiar & Melo, 2011	1	1	0	0
Paratetrapedia (*Paratetrapedia*) *moesta* (Cresson, 1879)	3	1	3	0
Scaptotrigona (*Gymnotrigona*) *hellwegeri* (Friese, 1900)	5	0	19	0
Tetrapedia maura Cresson, 1879	5	1	0	0
Triepeolus cameroni (Meade-Waldo, 1913)	3	0	2	1
Triepeolus epeolurus Rightmyer, 2004	0	0	1	0
Triepeolus laticeps (Friese, 1917)	0	0	0	2
Triepeolus sp. *complex* group	0	0	1	0
Triepeolus tepanecus (Cresson, 1878)	0	0	3	1
Trigonisca pipioli (Ayala, 1999)	11	0	1	0
Xenoglossa cacuminis (LaBerge, 2001)	0	0	16	0
Xenoglossa donata (Cresson, 1878)	0	0	15	5
Xenoglossa fastigiata (LaBerge, 2001)	0	1	14	1
Xenoglossa sp. 1	0	0	1	0
Xenoglossa (*Xenoglossoides*) *salviae* (LaBerge, 1989)	46	3	0	2
Xylocopa (*Notoxylocopa*) *guatemalensis* Cockerell, 1912	11	1	6	1
Xylocopa (*Schonnerrhia*) *muscaria* (Fabricius, 1775)	1	1	0	1
Colletidae				
Colletes sp. 1	1	0	0	0
Colletes sp. 2	1	0	2	0
Colletes sp. 3	0	0	1	0
Mydrosoma serratum (Friese, 1899)	5	1	0	0
Ptiloglossa sp. 1	1	0	0	0
Halictidae				
Augochlora (*Oxystoglossella*) *aurifera* Cockerell, 1897	3	4	0	2
Augochlora (*Oxystoglossella*) *cordiaefloris* Cockerell, 1907	8	0	8	0

Species	El Limón		Quilamula	
	Female	Male	Female	Male
Augochlora (*Augochlora*) *quiriguensis* Cockerell, 1913	1	0	0	0
Augochlora (*Augochlora*) *sidaefoliae* Cockerell, 1913	1	0	0	0
Augochlora (*Augochlora*) *smaragdina* Friese, 1917	2	2	4	1
Augochlorella neglectula (Cockerell, 1897)	6	0	7	2
Augochloropsis (*Augochloropsis*) *ignita* (Smith, 1861)	0	0	1	0
Augochloropsis (*Paraugochloropsis*) *metallica* (Fabricius, 1793)	6	1	6	0
Caenaugochlora sp. 1	1	0	0	0
Halictus (*Seladonia*) *hesperus* Smith, 1862	0	0	15	0
Halictus (*Odontalictus*) *ligatus* Say, 1837	15	0	20	6
Lasioglossum (*Lasioglossum*) *acarophilum* McGinley, 1986	4	0	0	0
Lasioglossum (*Dialictus*) sp. 1	6	0	2	0
Lasioglossum (*Dialictus*) sp. 2	2	1	0	1
Lasioglossum (*Dialictus*) sp. 3	1	0	1	0
Lasioglossum (*Dialictus*) sp. 4	0	0	1	0
Pseudaugochlora graminea (Fabricius, 1804)	1	0	1	0
Megachilidae				
Anthidiellum (*Loyolanthidium*) *apicale* (Cresson, 1878)	6	2	0	0
Anthidiellum (*Loyolanthidium*) *azteca* (Urban, 2001)	4	19	3	0
Anthidium (*Anthidium*) *maculifrons* Smith, 1854	0	0	1	2
Anthodioctes aff. lourdes Urban, 1999	3	0	0	0
Anthodioctes agnatus (Cresson, 1878)	12	1	0	0
Ashmeadiella (*Ashmeadiella*) *opuntiae* (Cockerell, 1897)	2	2	5	0
Atoposmia sp. 1	0	0	1	0
Coelioxys (*Cyrtocoelioxys*) *chichimeca* Cresson, 1878	0	0	0	1
Coelioxys (*Neocoelioxys*) *menthae* Cockerell, 1897	1	0	0	0
Coelioxys sp. 1	0	0	0	1
Coelioxys (*Leuraspidia*) *tepaneca* Cresson, 1878	0	0	0	1
Dianthidium (*Derachanthidium*) *bohartorum* Griswold & Michener, 1988	0	0	1	1
Dianthidium (*Adanthidium*) *discophorum* Griswold & Michener, 1988	13	7	0	1
Dianthidium (*Mecanthidium*) *macrurum* Cockerell, 1913	4	2	1	0
Heriades (*Neotrypetes*) *viridiana* Rojas-Arias, Griswold & Ayala 2025	20	1	4	0
Heriades (*Neotrypetes*) *nora* Rojas-Arias, Griswold & Ayala 2025	1	3	0	0
Hypanthidium (*Hypanthidium*) *mexicanum* (Cresson, 1878)	2	0	0	0
Lithurgopsis planifrons (Friese, 1908)	16	5	2	2
Megachile (*Chelostomoides*) *aff. abacula* Cresson, 1878	0	1	0	0
Megachile (*Sayapis*) *zapatlana* Cresson, 1878	0	0	0	2
Megachile (*Neochelynia*) *chichimeca* Cresson, 1878	5	0	11	1
Megachile (*Chelostomoides*) *exilis* Cresson, 1872	1	0	0	0
Megachile (*Argyropile*) *flavihirsuta* Mitchell, 1930	2	5	0	0
Megachile (*Sayapis*) *frugalis* Cresson, 1872	3	3	1	3
Megachile (*Litomegachile*) *lippiae* Cockerell, 1900	0	0	2	0
Megachile (*Litomegachile*) *pankus* Bzdyk, 2012	3	0	0	0
Megachile (*Leptorachis*) *petulans* Cresson, 1878	6	5	10	4
Megachile (*Sayapis*) *inimica* Cresson, 1872	0	3	0	0
Megachile (*Chelostomoides*) *quadridentata* Mitchell, 1930	0	1	0	0
Megachile (*Chelostomoides*) *reflexa* (Snelling, 1990)	0	16	0	4
Megachile (*Pseudocentron*) *azteca* Cresson, 1878	0	0	0	1

Species	El Limón		Quilamula	
	Female	Male	Female	Male
Megachile (*Chrysosarus*) sp. 1	1	0	0	1
Megachile (*Cressoniella*) *zapoteca* Cresson 1878	0	3	0	0
Megachile (*Pseudocentron*) *elongata* Smith, 1879	0	2	0	0
Megachile (*Chelostomoides*) *texensis* Mitchell, 1956	0	0	1	0
Osmia (*Diceratosmia*) *aliciae* Ayala & Griswold, 2005	2	0	0	0
Paranthidium (*Paranthidium*) *gabbii* (Cresson, 1878)	11	7	0	0
Paranthidium (*Paranthidium*) *vespoides* (Friese, 1925)	2	3	0	0
Stelis (*Dolichostelis*) *costaricensis* (Rchb.f. 1855)	0	1	0	2
Trachusa (*Heteranthidium*) *catinula* Brooks & Griswold, 1988	0	0	1	0
Trachusa (*Ulanthidium*) *mitchelli* (Michener, 1948)	4	14	0	0
Trachusa (*Heterantjhidium*) *pectinata* Brooks & Griswold, 1988	1	1	1	1
Trachusa (*Ulanthidium*) *pueblana* Thorp & Brooks, 1994	0	2	1	1

Table 2. Numbers of bees at two localities of the tropical dry forest in Mexico.

Family	Number of genera		Number of species		Abundance	
	El Limón	Quilamula	El Limón	Quilamula	El Limón	Quilamula
Andrenidae	3	4	12	12	26	62
Apidae	24	20	45	47	288	236
Colletidae	3	1	4	2	9	3
Halictidae	7	6	14	13	65	78
Megachilidae	13	11	32	25	234	75

The family Apidae was present the whole sampling period and was the most abundant with 524 individuals (49% of the total). Megachilidae was the second most abundant family with 309 individuals (29%). The least abundant was Colletidae (Table 2). The pattern of number of genera per family was similar: 26 from Apidae (47%), 15 from Megachilidae (26%), and only 3 from Colletidae (5%). *Megachile* was the genus with the most species (17), while 26 genera were each represented by one species. When considering bee abundance by season, it was highest during the 2015 rainy season in both localities (Fig. 2). In El Limón, bee abundance was highest in October (156 bees), followed by September (102 bees) (Fig. 2A). In Quilamula, September was the month with the highest abundance (Fig. 2B). Bee abundance was low during the dry season at both localities (Fig. 2). In fact, no bees were collected at either locality during March.

Bee abundance differed significantly across families, localities and seasons (chi-square = 255.5, d.f. = 15, P = 2.2e-16) (Fig. 3). Colletidae and Andrenidae were collected exclusively during the rainy season. According to the standardized residuals, the abundance of Andrenidae was higher than expected by chance during both rainy seasons at Quilamula; although the pattern was similar at El Limón, abundance was as expected by chance. The abundance of Halictidae did not differ significantly between

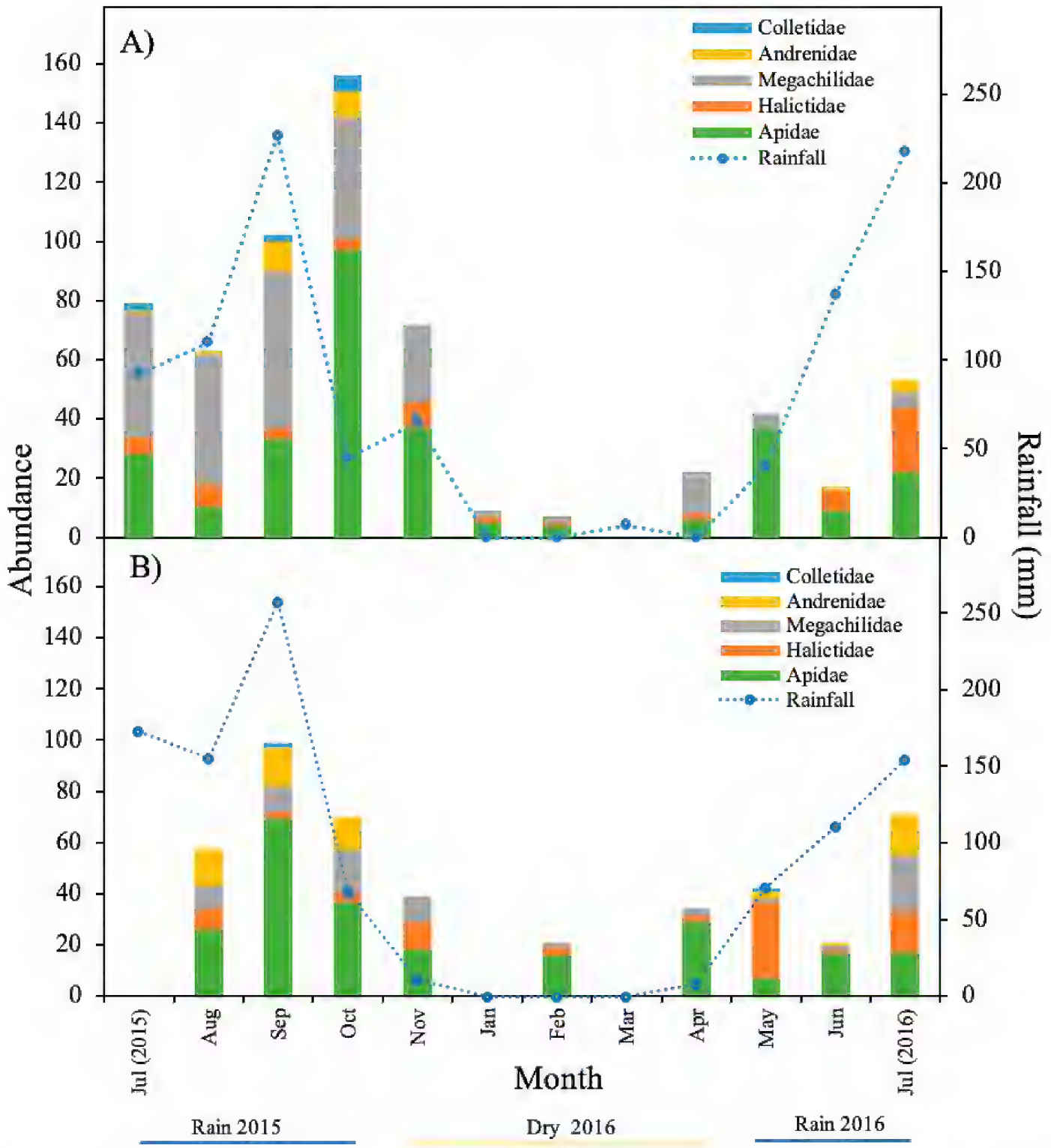

Figure 2. Bee seasonality per family in two sites of the tropical dry forest **A** El Limón **B** Quilamula. Dotted line indicates the mean monthly precipitation.

localities, but was significantly lower than expected during the 2015 rainy season and higher than expected during the 2016 rainy season. Megachilidae had higher abundance than expected in El Limón during the 2015 rainy season and lower abundance than expected in Quilamula during the same season. The abundance of Apidae was significantly higher than expectation in Quilamula during the 2015 rainy season and the dry season. Surprisingly, although high, abundance of Apidae was significantly lower than expected at El Limón during 2015 rainy season.

Bee sampling was sufficient in both localities and all three seasons, with sample coverage ranging from 92% to 100%. El Limón had 23% singletons and 8.1% doubletons, whereas Quilamula had 24.3% and 14.9% singletons and doubletons, respectively.

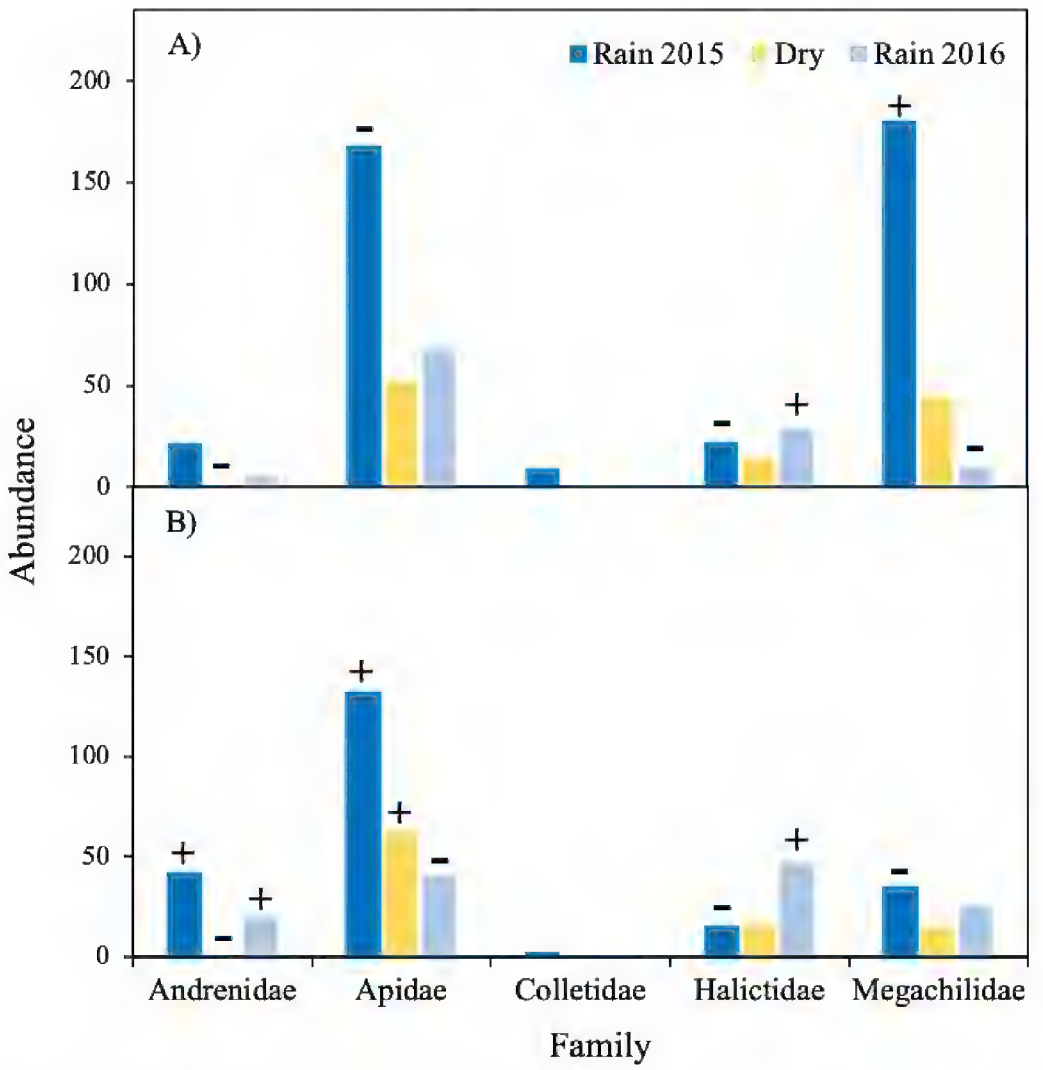

Figure 3. Bee abundance during the three seasons of study in **A** El Limón and **B** Quilamula. The positive and negative signs indicate that bee abundance was higher or lower than expected by chance, respectively. Rain 2015: from July to October 2015; Dry 2015–2016: from November 2015 to April 2016; Rain 2016: from May 2016 to July 2016.

These percentages of singletons and doubletons indicate a high incidence of rare species. There were no significant differences between localities in any of the three orders of diversity (Fig. 4).

When comparing diversity across seasons with localities pooled, we found that the 2015 rainy season had a higher diversity of the three orders than the other two seasons (Fig. 5).

When combining localities and seasons, diversity of the three orders was significantly higher at El Limón and Quilamula during the 2015 rainy season than in the remaining four communities (Table 3).

Table 3. Comparison of bee diversity (qD) between two sites of the tropical dry forest. 0D is the species richness, 1D is the diversity of effective species, and 2D is the diversity of rare species.

qD	El Limón			Quilamula		
	Rainy 2015	Rainy 2016	Dry 2016	Rainy 2015	Rainy 2016	Dry 2016
0D	76	13	18	73	9	17
1D	43.99	9.46	11.53	45.81	3.64	8.90
2D	29.42	7.70	8.87	31.50	2.35	6.43

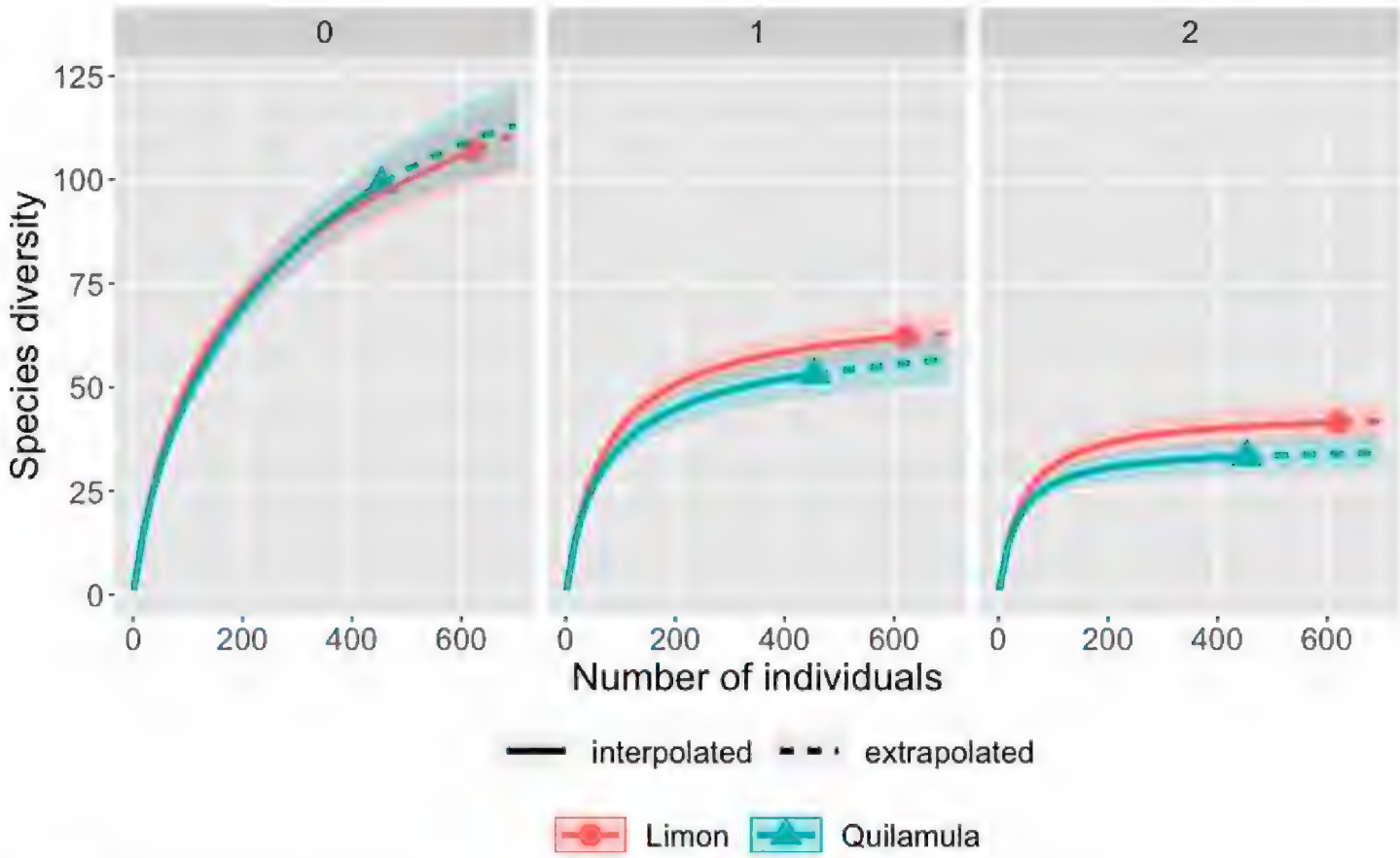

Figure 4. Diversity of bees between two localities of tropical dry forest in Mexico.

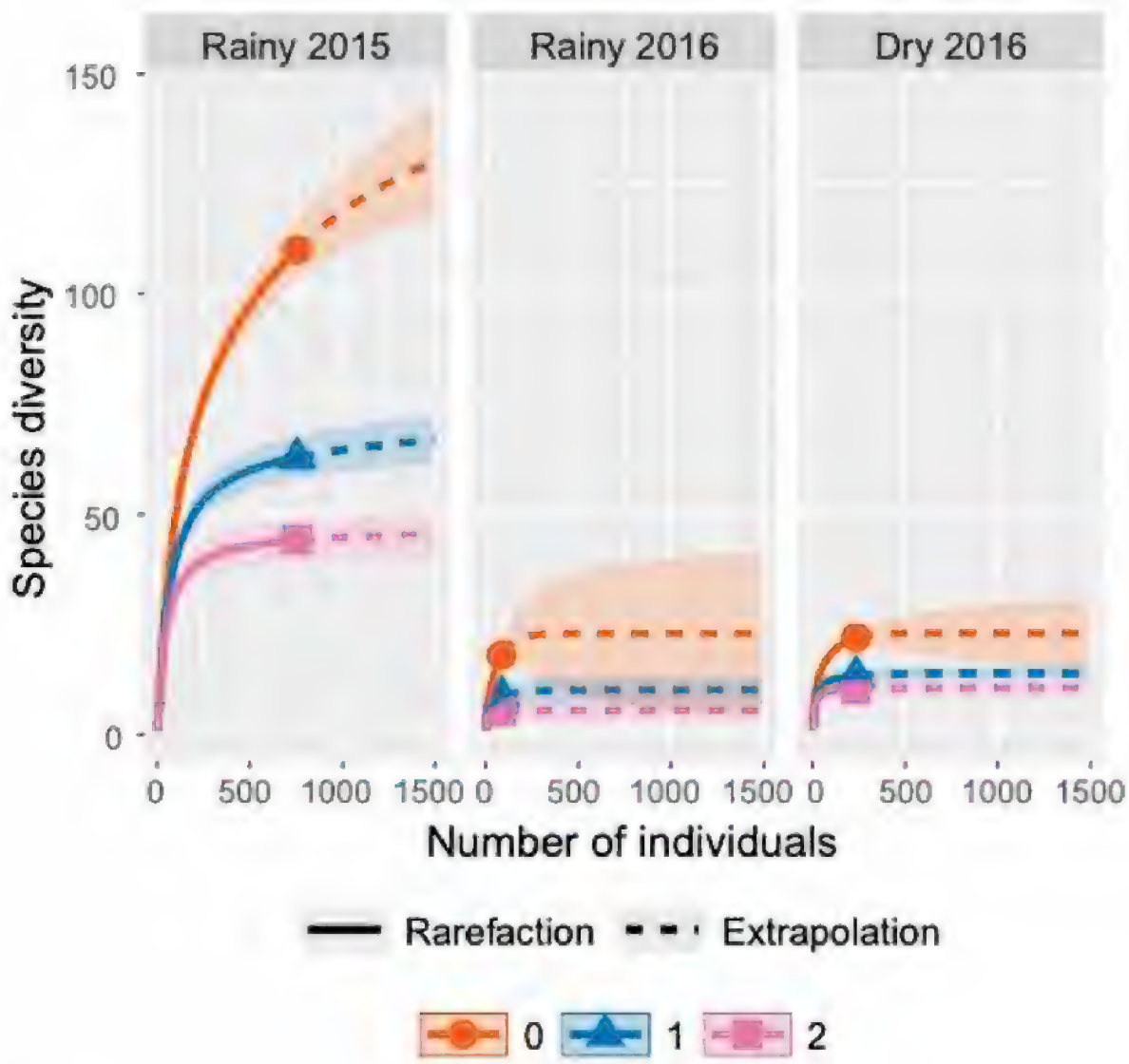

Figure 5. Diversity of bees among three seasons in the tropical dry forest. Seasons: rain 2015, from July to October 2015; Dry 2015–2016, from November 2015 to April 2016; Rain 2016, from May 2016 to July 2016.

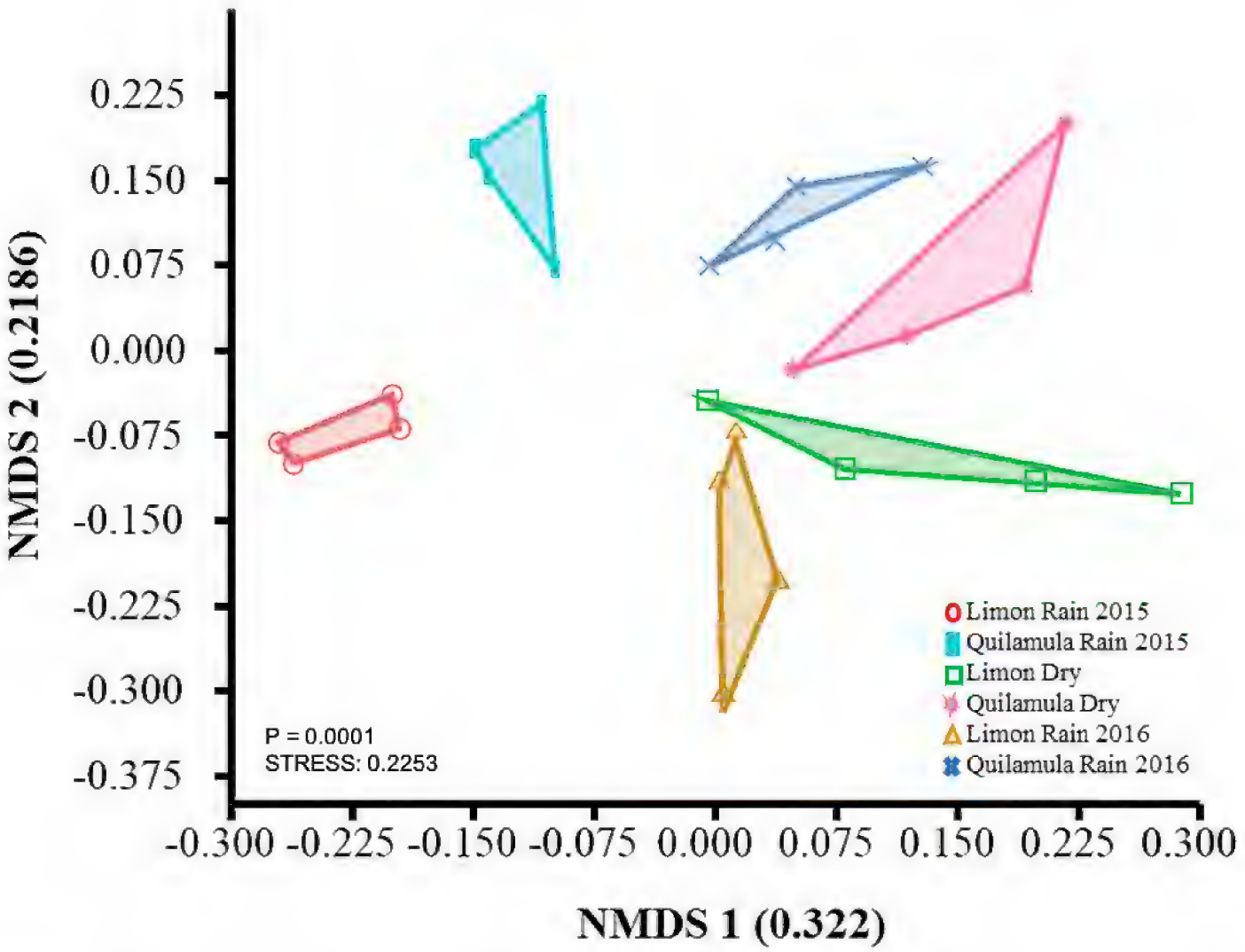

Figure 6. Non-metric multidimensional scaling (NMDS) ordinations illustrate the similarity of bee species composition across bee communities formed from the combination of the two localities and three seasons. Each point is a two-dimensional representation of bee species composition per locality on global-nonmetric multidimensional scaling (NMDS).

Only 57 species (39% of the total) were shared between localities. Fifty species were exclusive to El Limón and 42 to Quilamula. The results of the similarity of bee communities showed that NMDS ordination explained 54.1% of the variance (axis 1 = 32.2% and axis 2 = 21.9%), where each point is a two-dimensional representation of the composition of species in a single community based on global NMDS. The composition of bee species varied across the six communities (ANOSIM r = 0.90, P = 0.00001), and the post-hoc pairwise comparisons indicate that all of the pairwise differences were significant (Fig. 6). The moderate percentage of shared species between localities and the results of the community composition indicate that bee communities are heterogeneous across localities and seasons.

Discussion

Our sampling revealed a species richness similar to that reported in a study of tropical dry forest in Mexico (Razo-León e al. 2018), but lower than that found in other bee diversity studies conducted in Morelos State (Ayala et al. 1996; Hinojosa-Díaz 2003).

The two localities had distinct bee communities throughout the year, and within each locality, the bee community differed across seasons. Like other studies of bee diversity in tropical dry forests, we found that bee abundance is linked to the period of rainfall (Poveda-Coronel et al. 2018; Kammerer et al. 2024). The highest bee abundance was found during the rainy seasons, which is when there is higher abundance of flowering resources. Aside from precipitation, it has been documented that vegetation cover influences the diversity of bees (Liow et al. 2001; Winfree et al. 2010; Kammerer et al. 2024). Our analysis of MSAVI showed that the sampling area in El Limón had more understory vegetation cover, suggesting a higher abundance of herbs and annual plants in the sampling sites. This pattern is likely due to differences in land management practices and the conservation status of El Limón as part of the REBIOSH. Although no significant differences in bee diversity were found between the localities, we did observe differences in bee community composition. This may be linked to the availability and quality of floral and non-floral resources in each locality.

Apidae was the most abundant family in the whole study, like other studies, as it is the most diverse bee family. Apidae showed notable abundance at both localities during the first rainy season. In fact, the two highest abundance records of the whole study were in October at El Limón: *Xenoglossa salviae* (n = 30, a specialist on *Salvia* [Lamiaceae]), and *Bombus steindachneri* (n = 28). This locality had a high abundance of annual plants, in particular *Salvia* sp. and *Tithonia* sp. [Asteraceae] (pers. obs.). Apidae was the most abundant family during the dry season, with significantly higher counts in Quilamula. The abundance of Apidae during the dry season is due to polylectic species such as *Xylocopa fimbriata* and *X. guatemalensis*, each with 11 individuals during the whole dry season. The presence of *Xylocopa* during the dry season may be related to the blooming of *Ipomoea* species, which provide abundant floral resources and have been documented as floral hosts of *Xylocopa* (Bullock et al. 1987).

The family Megachilidae was the second most abundant. Megachilidae showed notably high abundance in El Limón during the first rainy season, but significantly lower in Quilamula during the same period. This may be related to differences between the localities aside from total vegetation cover, such as the intensity of land use management (Fig. 1). Potts et al. (2003) found that species richness of Megachilidae was positively associated with the availability of nectar and pollen. Many Megachilidae species (such as *Dianthidium* and *Anthidiellum*, Chui et al. 2021) depend on non-floral resources to construct their nests, such as leaf-pieces, resins, wax, oils, pebbles, and sand, which are provided more feasibly by woody vegetation (Requier and Leonhardt 2020). Hence, Megachilidae seems to be related to a diverse array of high-quality resources, including floral and non-floral. Further research is necessary to determine a potential link between habitat quality and megachilid diversity.

The family Andrenidae was present only during the rainy season at both localities, and it was significantly more abundant in Quilamula during both rainy seasons. Several members of Andrenidae have been related to herbaceous plants (Larkin et al. 2008; Wood et al. 2021) with a preference for foraging on annual plants (Potts et al. 2003) such as Asteraceae. Hence, although Quilamula had lower vegetation cover, the increased

land use for agricultural activities may have promoted an array with a higher proportion of annual plants and weeds, which in turn supported the abundance of Andrenidae.

Halictidae had a significant high abundance during the two rainy seasons at both localities. All species of Halictidae in this study belong to the subfamily Halictinae, which contains species that are relatively small (Michener 2007) and polylectic (Engel 2000; Dikmen 2007; Shebl 2012; Dalmazzo and Vossler 2015). These traits likely allow them to easily associate with herbs and annuals, like Andrenidae. This preference for foraging on herbs and annuals enables Andrenidae and Halictidae to be abundant in both localities, regardless of the vegetation cover.

Finally, Colletidae was the least abundant family, consistent with findings from other studies (Ramírez-Freire and Quiroz-Martínez 2016).

Two of the six locality-season communities showed differences in bee diversity. We found a higher diversity at the three orders during the 2015 rainy season at both localities, than in the dry season and the 2016 rainy season. These differences in diversity could be associated with a greater floral resource availability during the first rainy season. Sampling ended in July 2016 due to financial issues; hence, sampling of the 2015 rainy season comprised four months (July to October), whereas that of the 2016 rainy season only three months (May to July). Besides, the 2015 rainy season encompassed the months with higher precipitation and the end of the rainfall (which allowed a greater growth of herbaceous plants), while the 2016 rainy season included only the onset of rainfall. Flowering of herbaceous and annual plants from the tropical dry forest depends directly on precipitation, hence an important proportion of floral resources of this stratum is available during or after the rains. During the dry season, flower availability from herbaceous vegetation is scarce, and our sampling was focused on understory vegetation. Floral density during the dry season comes from trees and shrubs (e.g. *Ipomoea*, Ayestarán-Hernández 2010; Fabaceae, López-Reyes 2019; *Opuntia* species, pers. obs.), providing important floral resources for bee community and other floral visitors (González-Leiva 2024). Habitats may vary widely in both the timing and magnitude of floral and nesting resources available to bees (Ogilvie and Forrest 2017), leading to seasonally variable interactions between bee communities and surrounding land use (Cole et al. 2017; Galpern et al. 2021). These differences in floral resource availability across vegetation layers (canopy and understory) suggest that the bee diversity we find was a subset of the total bee diversity at these sites. These potential differences highlight the need for further research on bee diversity specifically associated with tree strata. Such studies would deepen our understanding of seasonal shifts in bee communities between dry and rainy seasons, as well as differences between canopy and understory vegetation in tropical dry forests.

We did not find significant differences when comparing the three orders of diversity between localities. This means that both localities have the same species richness, and the same number of rare and effective species, despite differences in herbaceous cover vegetation. The number of effective species in El Limón tended to be higher than in Quilamula, but this difference was not significant. More extensive sampling could inform whether El Limón has a higher evenness of the bee community than Quilamula.

Bee communities are commonly structured by rare species despite intensive sampling, since between 16 to 42% of the species are singletons (24% in our study; Williams et al. 2001). This high proportion of rare species is common in arthropod communities of tropical forests, partly on account of undersampling (Coddington et al. 2009; Cardoso et al. 2009; Burington et al. 2020). However, our sampling was efficient, higher than 90% in each locality. Aside from undersampling, the high number of singletons suggests a widespread pattern of species rarity in bee communities, where factors such as habitat heterogeneity, patchiness of floral resources, life history traits of bee species, and even disturbance, certainly contribute to this pattern (Williams et al. 2001; Potts et al. 2003).

Despite the few differences in diversity of the three orders, we found that composition of the bee communities significantly differed among localities, seasons, and their combination. Particularly, the community composition during the 2015 rainy season (with both localities pooled, data not shown), and that of El Limón during the 2015 rainy season (Fig. 6), were more different than the remaining communities, indicated by the distance of the resulting polygons. We also found that El Limón and Quilamula shared only 39% of the species, meaning that almost half of each community's species are exclusive for each site. Evidence suggests that in landscapes with moderate disturbance, such as agricultural zones, generalist bee species and those tolerant to disturbance are the primary beneficiaries (Harrison et al. 2019). Community composition may show a high variability among sites, mostly in relation to bee life traits such as body size, nesting preferences, floral preferences, and even social habit (Winfree et al. 2007; Ramos-Fabiel et al. 2019). We expected to find lower diversity in Quilamula, given the higher intensity of land use for agriculture and livestock. Quilamula had lower cover vegetation and a higher proportion of the land used for agriculture, but bee diversity was equal to that of El Limón. Two factors could explain this similarity. The negative relationship between bee diversity and disturbance is notable only when levels of disturbance are highly contrasting (reviewed in Winfree et al. 2009). In tropical systems, low-intensity farming practices, combined with forested landscapes, help preserve a significantly greater diversity of bees compared to agricultural systems characterized by high-intensity farming and severe deforestation (Vides-Borrel et al. 2019). Besides, land use intensity does not affect all bee species equally (Klein et al. 2002), there are specific responses of each bee taxon depending on their food requirements, sites and materials for building their nests and thermoregulation capacities (Brosi et al. 2008). Hence, it is possible that differences in land use were not so marked between the studied localities to account for differences in bee diversity, and that agriculture and livestock practices in Quilamula allow the presence of a notable diversity of bees.

It has been found that bee communities have an elevated turnover, even on a local scale (Williams et al. 2001). Hence, for conservation purposes, the high species turnover imposes difficulties when protecting species based on area coverage. El Limón is protected as part of the REBIOSH. However, for sites of tropical dry forest with intensive land-management like Quilamula, bee conservation strategies should focus on practices that positively impact at medium and local scales. So, conservation strategies where agricultural and livestock practices are present should ensure the availability of

floral and nesting resources. For example, allowing the growing of wildflower plantings adjacent to flowering crops (Williams et al. 2015), favoring silvopasture systems (Odanaka and Rehan 2020), and ensuring the conservation of older successional stands of forest (Ramos-Fabiel et al. 2019), among others.

A total of 148 species were collected, a lower species richness reported previously in two studies conducted in Morelos state. Ayala et al. (1996) reported 209 species, and Hinojosa-Díaz (2003) reported 197 species plus 138 morphospecies. These data suggest that despite the small size of the state of Morelos, the melittofauna could represent up to 10% of the Mexican melittofauna. Bee species richness in Morelos state could be related to the heterogeneity of its ecosystems, as well as the high plant diversity reported in the tropical dry forests. This study contributes to the knowledge of the diversity and seasonality of the wild bee community in a tropical dry forest of central Mexico. Although the comparison between localities with different cover of herbaceous vegetation did not render significant differences in bee diversity, we did find significant differences in species composition as well as that seasonality is an important factor that structured the bee community in the studied localities.

Data availability

The authors confirm that the data supporting the findings of this study are available within the article.

Author contribution

The study conception and design were conducted by CM-P. Material preparation and curation, CM-P and HEF-L. Bee identification, HEF-L. Analyses were performed by CM-P, KMA-D, KS-E and IV-E. The first draft of the manuscript was written by CM-P and KMA-D. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Conflict of interest

The authors declare that they have no conflict of interest.

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